Z. Säugetierkunde **64** (1999) 19–29

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Daylight behaviour of Humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa

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Receipt of Ms. 17. 12. 1997
Acceptance of Ms. 19. 08. 1998

Abstract

Data on the daylight behaviour of humpback dolphins *Sousa chinensis* were collected during sea- and land-based surveys undertaken in Algoa Bay, Eastern Cape, South Africa, throughout a three year period. Dolphin activities/behaviour were categorised as: "feeding", "travelling", "opportunistic feeding", "socialising and playing", "resting" and "other". It seems apparent that behaviour determines the spatial geometry of the dolphin group, but not the group size. The surfacing-breathing interval is similar for "feeding", "opportunistic feeding", and slow "travelling", but differs considerably from the pattern displayed during fast "travelling". Daylight behaviour of humpback dolphins is dominated by "feeding" and shows a regular pattern which is probably governed by the diurnal cycles of their prey. Generally, "feeding" peaks in the morning and gradually decreases through the rest of the day. As "feeding" decreases, "travelling" and "opportunistic feeding" increase, both peaking in the afternoon. "Resting" and "socialising and playing" occur with similar frequency throughout the day. This pattern varies little between summer and winter, as does the overall proportion of daylight behaviours. The only significant seasonal difference is in the frequency of "social/sexual" behaviour which peaks in summer. Although tidal cycle influences to some extent the behaviour of humpback dolphins, in Algoa Bay their daylight activity/behaviour is predominantly governed by time of day.

Key words: *Sousa chinensis*, daylight behaviour pattern, seasonal variation.

Introduction

Activity rhythms of animals represent an adaptation to seasonal and diurnal variations of environmental factors and are a result of a complex compromise between optimal foraging/feeding time, social activities, and environmental constraints (Cloudsley-Thompson 1961; Nielsen 1983). Diurnal and seasonal patterns of activity and behaviour have been described in detail for several terrestrial mammals. There is, however, a disproportionate lack of similar information concerning cetaceans (for review see Klinowska 1986; Shane et al. 1986). One reason for this lies in the practical difficulty of studying the behaviour of free-ranging cetaceans.

Humpback dolphins *Sousa chinensis* inhabit Indo-Pacific coastal waters and are known to occur along the east and south coast of South Africa (Ross et al. 1994). Despite its inshore occurrence, there has been little study of this species and much of our knowledge is based on fragmentary information. Only recently has the natural history of humpback dolphins been investigated in detail in the Algoa Bay region on the south Eastern Cape coast of South Africa (Karczmarski 1996). This long term study, although

0044-3468/99/64/01 – 019 $ 12.00/0

not strictly behavioural in its design, included many hours of observations and provided a good opportunity to collect observational data on dolphin behaviour. It was possible to quantify the daylight activity pattern of humpback dolphins and examine the daytime, seasonal, and tidal variations in their behaviour. Not only are these observations important in themselves, but they provide a valuable insight into the daily lives of this coastal dolphin. Furthermore, a better understanding of the ecological determinants of humpback dolphin behaviour may help in the development of appropriate protective measures for this little known and apparently threatened (Klinowska 1991) species.

Material and methods

Algoa Bay is the easternmost and largest of several shallow (mean depth < 50 m), log spiral bays found on the south-east coast of South Africa (Fig. 1). The Bay, flanked on the western side by Cape Recife (34°02′ S; 25°42′ E) and on the eastern side by the less prominent Cape Padrone (33°46′ S; 26°28′ E), is located along a generally exposed coastline and represents an open habitat with few surface geographical boundaries.

The behaviour of humpback dolphins was recorded during land- and sea-based surveys undertaken in the south-western part of Algoa Bay between May 1991 and May 1994. Daily land-based surveys usually started 1–2.5 hours after sunrise (weather permitting) and observations of the inshore waters, to approximately 1 km offshore, were carried out from several visually overlapping vantage points. Sea-based surveys were opportunistic, limited by both the presence of dolphins and weather conditions and were conducted using a 3.5 m inflatable boat powered by a 30 HP outboard engine.

The activity/behaviour of the focal group of dolphins (sensu Altmann 1974) was usually recorded at the commencement of each sighting and, thereafter, randomly for five minute intervals throughout the survey. For each of the five minute intervals, the lenght of time spent in different behaviours (see below) was estimated in the form of percentage. The raw field data were subsequently grouped into hourly intervals according to the time of day and into four tidal periods (1/2 low, low, 1/2 high, high) in which they were collected. During boat surveys, recording of dolphin behaviour began only after the animals were assumed to have become habituated to the presence of the boat – in most cases at least 30 minutes from the initial sighting and with the boat at a distance of 10–20 meters from the group. It was assumed that this gave the animals time to resume their normal activity (see also Acevedo 1991; Ballance 1992).

Generally, because aggregations of humpback dolphins were small (mean = 7 dolphins, sd = 2.52; Karczmarski 1996; Karczmarski et al. 1998) the whole group was often the focus of observations and it was possible to categorise the behaviour of the group as a whole (the predominant activity of the majority of the group members). Six broad categories of behaviour were distinguished:

The first category consisted of frequent and asynchronous dives, in varying directions, in one location, with an evident lack of directional movement; surfacing and respiration displayed no obvious pattern. During this activity dolphins often chased fish and occasionally fish capture was seen. Consequently, it is likely that this complex of behaviours represents feeding and is therefore referred to as "feeding".

The second category was characterised by persistent, directional movement, with all group members diving and surfacing synchronously. Chasing of fish or even social behaviour was extremely uncommon during this behaviour and, consequently, it is referred to as "travelling".

The third category appeared to be a combination of the previous two. Dolphins moved slowly, but usually in a fairly consistent direction. However, surfacing and diving were apparently less synchronised than during apparent "travelling". Furthermore, the directional movement was frequently interrupted by short bouts of localised movement (frequent changes in direction with no evident overall direction), during which some individuals performed long dives. Occasionally chasing of fish was seen. Social activity during this behaviour was uncommon. It was assumed that this pattern of activity represented "opportunistic feeding" and it is referred to as such.

The fourth category consisted of various vigorous activities including leaping out of the water, riding waves in the surf zone, high speed movement with frequent direction changes, and prolonged body contact with other dolphins. These were frequently accompanied by prolonged bouts of almost constant physical contact between two or more dolphins, which seemed to have a sexual meaning (see also

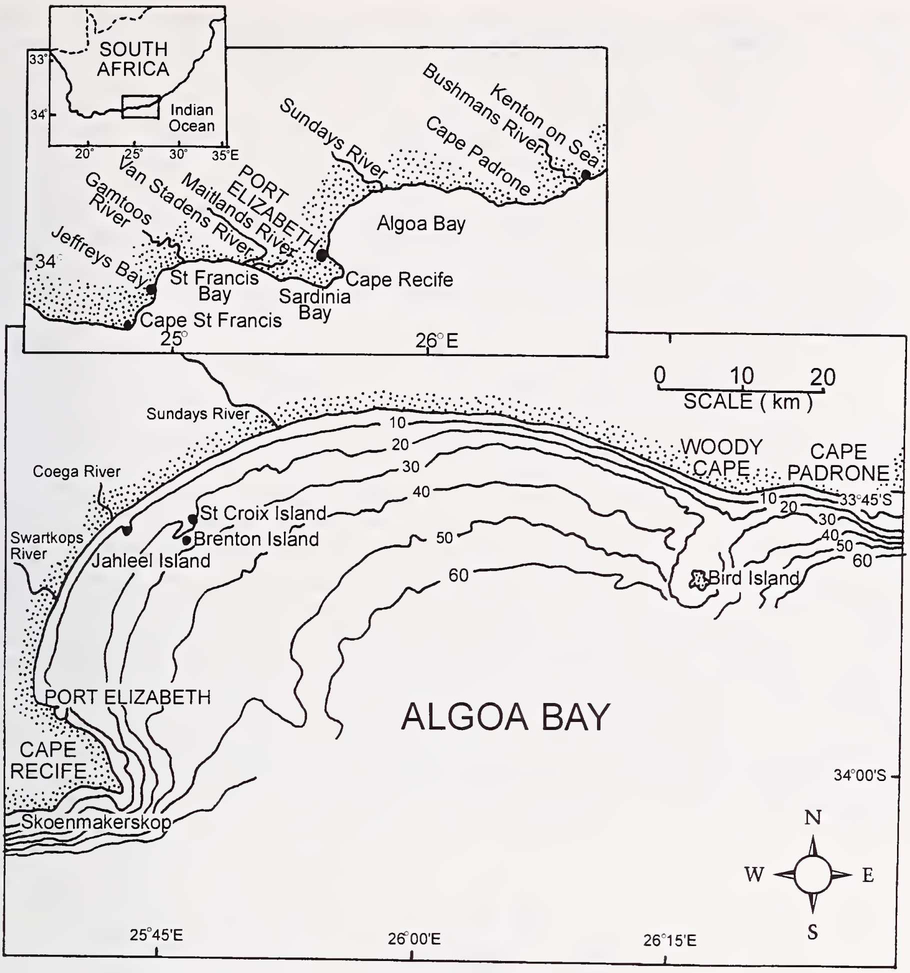

Fig. 1. The Algoa Bay study area on the south Eastern Cape coast of South Africa.

Karczmarski et al. 1997). It seems most likely that these activities served a social function and are referred to as "socialising and playing".

The fifth category consisted of a low level of activity, with the dolphins apparently floating stationary and motionless at the surface, with some occasional slow forward movement. This is referred to as "resting".

Activities which could not be easily assigned to any of the above categories were termed "other".

No underwater observations were conducted and dolphin behaviour is described as it was observed from the research boat. The spatial geometry of the dolphin group (after Shane 1990 a), its size, composition, and locality were noted at the commencement of each sighting and when any variable changed.

Two seasons. summer and winter, are distinguished here. "Summer" is defined as the period when the mean temperature of the inshore surface water is higher than the annual mean (18 °C). The period when the surface water temperature drops below this annual mean is referred to as "winter". In general, the first days of May mark the beginning of "winter" and late October marks the beginning of "summer".

The term "group" refers to any aggregation of more than one dolphin, including all age classes, within visual range of the survey team. Typically, these animals were in apparent association and engaged in similar activities for most of the observation period. Each time a group was observed, it was recorded as a "sighting". The term "sighting", however, has a wider meaning and includes solitary animals.

Results

Groups and solitary humpback dolphins were observed 104 times during more than 300 hours of observations. Dolphin behaviour was specifically recorded for a minimum of one hour during 83 sightings, for a total of 270 hours. In most instances, behaviour was recorded for between three and four hours (mean = 3.2 h), though the longest session exceeded six hours.

Groups of humpback dolphins varied in size from three to 24 animals with a mean of seven (sd = 2.52). Solitary individuals were seen frequently and constituted 15.4 % (n = 16) of sightings (see also Karczmarski et al. 1998). In most cases the size of groups remained unchanged throughout observations and was not affected by the animals' behaviour (Kruskal – Wallis ANOVA, KW = 39.57, n = 361, p = 0.53). Group geometry, however, was not random but varied according to activity. During "feeding", the dolphins were usually widely dispersed, with the distances between individuals varying constantly and ranging between approximately 1 m and at least 100 m. When "travelling", humpback dolphins formed a tight "single-file group", or fairly compact, oval shaped aggregation with the distance between individuals seldom exceeding a body-length of an adult dolphin (circa 2.5 m). The position of individuals within such groups, however, changed continually. During "opportunistic feeding" group geometry was not well defined, with dolphins moving in the same direction, but in a fairly dispersed aggregation; less dispersed, however, than during "feeding" (the max. distance between individuals usually < 50 m). Similarly, humpback dolphins did not display any consistent group geometry during "socialising and playing" or "resting". The distances between individuals changed continually, ranging between a "touching distance" when body contact was performed and circa 25 m.

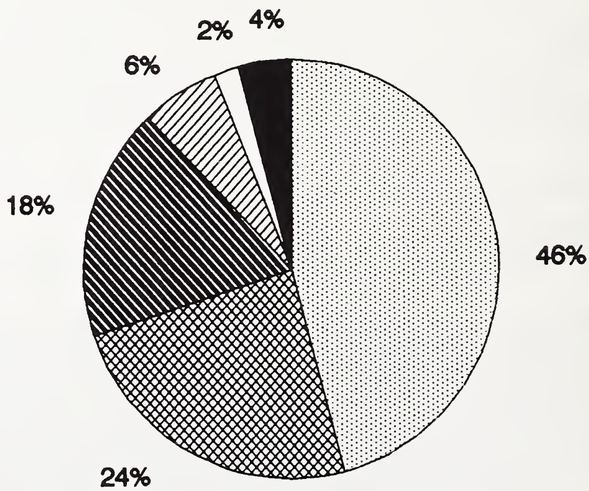

Fig. 2. The mean proportion (%) of daylight hours spent by humpback dolphins in each of six behaviours (dotted – feeding, cross-hatched – travelling, dense hatched – opportunistic feeding, hatched – socialising and playing, open – resting and black – other) in Algoa Bay between May 1991 and May 1994.

The surfacing-breathing interval did not vary significantly between "feeding" (mean = 25.6 sec., n = 36, sd = 17.3), "opportunistic feeding" (mean = 30.1 sec., n = 27, sd = 11.8) and slow "travelling" (mean = 23.3 sec., n = 29, sd = 7.1); (Kruskal – Wallis ANOVA, KW = 17.44, n = 92, p = 0.61). During these behaviours humpback dolphins ventilated by rolling at the surface with an overall mean interval of 26.3 sec. (sd = 12.7). This pattern changed considerably during fast "travelling" (n = 27), when several (4 to 9, mean = 6, sd = 1.7) rapid ventilations separated by only a few seconds (mean = 8.6 sec., sd = 4.1) alternated with a long submergence of mean duration = 101.3 sec. (sd = 20.9), during which a long distance was travelled at high speed.

The daylight activity of humpback dolphins in Algoa Bay was dominated by "feeding" (Fig. 2). Behaviours classified as "feeding" and "opportunistic feeding", if combined, contributed well over 50 % of all recorded activities. "Travelling" represented the second most frequently seen behaviour, while "resting" or "socialising and playing" were infrequent and accounted for less than 10 % of the dolphins' daylight activities.

Humpback dolphins in Algoa Bay displayed little seasonal difference in the proportion of diurnal behaviours (Fig. 3). Although dolphins appeared to spend more time "feeding" in winter and, inversely, less time on "opportunistic feeding", none of these differences were significant (Mann-Whitney, U = 87.50, n = 83, p = 0.38 and U = 95.00, n = 83, p = 0.20, respectively). The proportion of combined "feeding" and "opportunistic feeding" was similar for both summer (63.0 %) and winter (64.3 %). The only signifcant seasonal difference was for "socialising and playing" (Mann-Whitney, U = 105.00, n = 83, p = 0.05) (Fig. 3). The summer frequency of "socialising and playing" was double that of winter. The sexual component of this behaviour was also significantly greater in summer (47.2 %) than in winter (11.3 %) (Mann-Whitney, U = 240.00, n = 65, p < 0.0001).

The proportion of daylight hours spent in different behaviours was well defined and varied significantly throughout the day (Fig. 4) for both summer (Kruskal – Wallis ANOVA, n = 181, KW = 57.08, p < 0.0001 for "feeding": KW = 56.72, p < 0.0001 for "travelling"; KW = 25.89, p = 0.007 for "opportunistic feeding"; KW = 35.69, p = 0.0002 for "so-

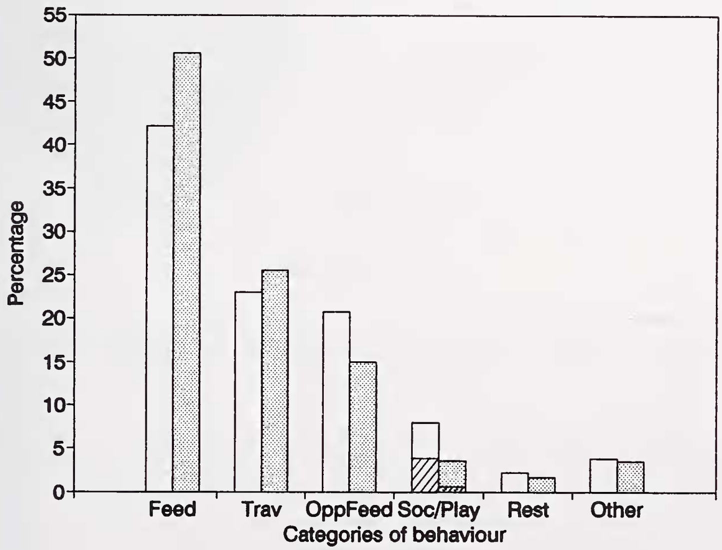

Fig. 3. Seasonal (☐ – summer and ░ – winter) variation in the mean proportion (%) of diurnal behaviours displayed by humpback dolphins in Algoa Bay between May 1991 and May 1994. Sexual behaviour (▨) as a proportion (%) of socialising and playing is also shown.

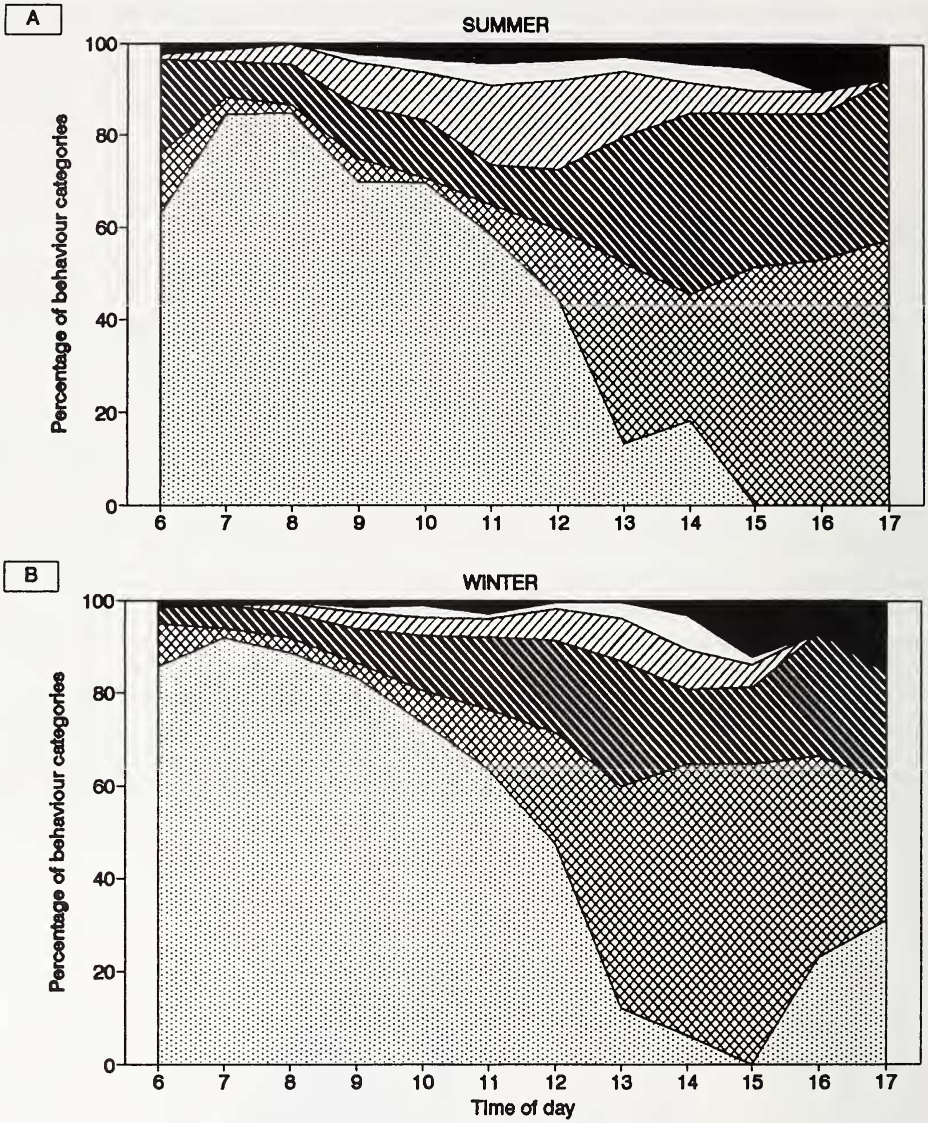

Fig. 4. The mean hourly proportion (%) of the diurnal behaviours ([dotted] – feeding, [cross-hatched] – travelling, [dark diagonal] – opportunistic feeding, [light diagonal] – socialising and playing, [white] – resting and [black] – other) of humpback dolphins observed in Algoa Bay between May 1991 and May 1994 for both summer (A) and winter (B).

cialising and playing" and KW = 31.87, p = 0.0008 for "resting") and winter (Kruskal – Wallis ANOVA, n = 102, KW = 62.15, p < 0.0001 for "feeding"; KW = 59.20, p < 0.0001 for "travelling"; KW = 27.96, p = 0.003 for "opportunistic feeding"; KW = 33.21, p = 0.0005 for "socialising and playing" and KW = 24.31, p = 0.01 for "resting"). Generally, "feeding" peaked in the morning and gradually decreased through the rest of the day. As "feeding" decreased, "travelling" and "opportunistic feeding" increased, both peaking in the afternoon. During winter evenings the frequency of "travelling" and "opportunistic feeding" decreased again, with a corresponding secondary increase in "feed-

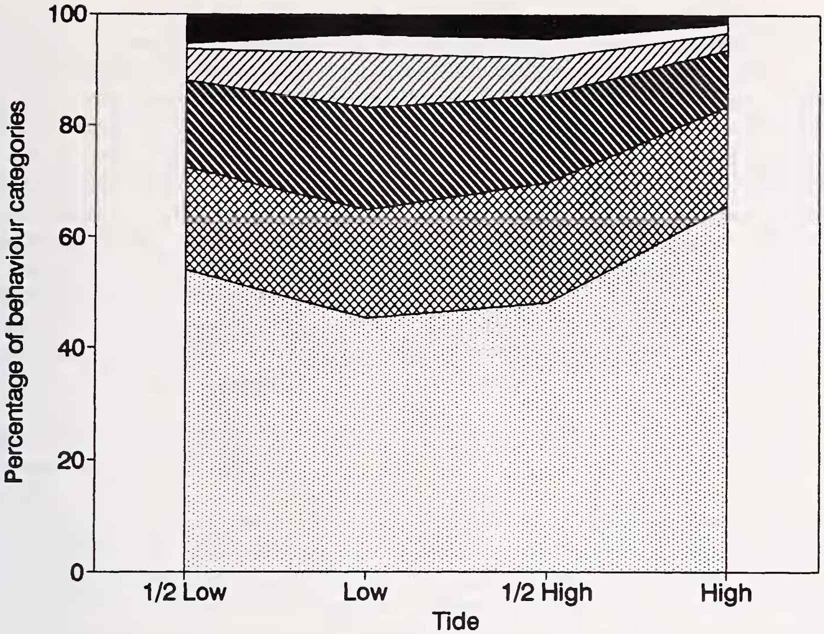

Fig. 5. Tidal influence on the diurnal behaviours (▒ – feeding, ▒ – travelling, ▒ – opportunistic feeding, ▒ – socialising and playing, ☐ – resting and ■ – other) of humpback dolphins in Algoa Bay observed between May 1991 and May 1994.

ing". Prolonged bouts of "resting" and "socialising and playing" occurred with similar frequency throughout the day, but were slightly less evident in the morning and evening. There was, however, a clear summer increase in "socialising and playing" behaviour around midday.

The behaviour of humpback dolphins in Algoa Bay did not appear to be significantly related to the tides (Fig. 5), except for "feeding" which increased during high tide (Kruskal – Wallis ANOVA, KW = 27.85, n = 102, p = 0.05).

Discussion

The six categories of behaviour distinguished in the present study are generally consistent with the types of behaviour observed and classified in several other studies (Saayman and Tayler 1979; Shane 1990 a, b; Ballance 1992; Brager 1993). Behaviour of humpback dolphins in Algoa Bay appeared to determine the spatial geometry of the group in a similar way as has been observed for other cetaceans (Shane 1990 a; 1995) which suggests a functional significance. The tight structure of a "travelling" group may possibly reduce the likelihood of incidental separation of an individual from the group, increase the sensory invigilation of the area being travelled through and possibly (as observed by Saayman and Tayler 1979) facilitate an active, co-operative defence. Furthermore, because swimming at the surface seems to require 4.5 times more energy than swimming at a depth of about one-half of body length (Au and Weihs 1980; Hui 1987) the long distance covered underwater during fast "travelling" is likely to be energetically beneficial (Hui 1989).

The close proximity of group members during "resting" could possibly increase safety of an individual due to sensory integration of a group (e. g. Norris and Dohl 1980 a). The dispersed geometry of groups engaged in "feeding" and "opportunistic feeding" on the other hand, appears to be related to the foraging/feeding behaviour used by the animals (Würsig 1986). The widely dispersed "feeding" groups indicate that individual, rather than co-operative, feeding is likely to be the norm for humpback dolphins in Algoa Bay.

Feeding dominated the daylight activity of humpback dolphins in Algoa Bay, as has also been observed for bottlenose dolphins in the bay system of Galveston, Texas (Brager 1993). However, the overall proportions of daylight behaviours recorded for humpback dolphins during the present study vary considerably from those described by Saayman and Tayler (1979) for humpback dolphins in Plettenberg Bay. The proportions of time dolphins were seen feeding (26.5 %) and travelling (50 %) in Plettenberg Bay are almost the reverse of those in Algoa Bay. One reason for this could be that, despite an apparently similar definition of behaviour categories, the actual classification of behaviour observed in the field differed considerably between the two studies. Alternatively, it is possible that there are several other factors which differ between Algoa Bay and Plettenberg Bay.

The time spent on non-feeding behaviours appears to be proportional to feeding efficiency (Herbers 1981). As feeding efficiency increases, less time is spent searching for or capturing prey and more time is available for less active behaviour. Feeding efficiency is likely to increase with richness of habitat and, inversely, more time is likely to be required for feeding where food is not so plentiful. Consequently, the overall proportion of diurnal behaviours is likely to be a function of the habitat and biological needs of the animals and the considerably smaller proportion of daylight hours occupied by feeding in Plettenberg Bay may reflect a greater abundance of the inshore prey resources.

Furthermore, as discussed in Karczmarski (1996), the Plettenberg Bay region houses a multitude of shallow rocky reefs which facilitate feeding for humpback dolphins. In contrast, only the south-westerly bight of Algoa Bay has abundant shallow reefs. Consequently, it is possible that humpback dolphins use the areas of Algoa Bay and Plettenberg Bay differently, with several feeding sites in the Plettenberg Bay region; but apparently only one (limited in size) primary feeding ground in Algoa Bay, where feeding is particularly intensive. By comparison, the overall proportion of daylight behaviours observed for bottlenose dolphins *Tursiops truncatus* on their estuarine feeding grounds in the Gulf of California, Mexico (Ballance 1992) is strikingly similar to that of humpback dolphins in Algoa Bay. On the other hand, the proportion of time humpback dolphins spent feeding and travelling in Plettenberg Bay is strikingly similar to that reported by Ballance (1992) for bottlenose dolphins when the animals were away from their estuarine feeding grounds.

Humpback dolphins in Algoa Bay displayed little seasonal difference in the overall proportion/frequency of daylight behaviours. Only "social" and "sexual" behaviour showed a seasonal difference, increasing in summer. This corresponds with the summer peak of calving observed for humpback dolphins in Algoa Bay (Karczmarski 1996) and, consequently, supports the one year gestation period suggested for this species (V. G. Cockcroft, unpubl. data). Similarly, a seasonal (spring and summer) increase in social behaviour, as well as abundance of calves, was observed for bottlenose dolphins off the Texas coast (Shane 1990 b).

The general lack of seasonal variation in the overall frequency of other behaviours – particularly feeding – is surprising, considering possible changes in energy requirements of the dolphins due to declining water temperature (Cockcroft and Ross 1990; Ross and Cockcroft 1990). There was, however, an apparent increase in feeding behaviour during winter evenings in Algoa Bay, which may possibly reflect an increased energetic demand of the dolphins or, alternatively, an increase in prey abundance on winter evenings Because of early nightfall in winter, all evening observations were discontinued between 17h00 and 18h00 (compared to 19h00–20h00 in summer). In winter, however, the secondary feeding peak increased at this time, while no feeding was observed during evenings in summer. Consequently, it is possible that in winter feeding occupies a larger proportion of humpback dolphin activity than was apparent during the present study.

The proportion of daylight which humpback dolphins used for different behaviours varied considerably throughout the day and formed a distinct diurnal pattern. This pattern seems to follow the solar day and is, possibly, to a large degree shaped by the diurnal cycles of the prey species. A similar phenomenon is apparent for several populations of coastal bottlenose dolphins (Saayman et al. 1973; Würsig and Würsig 1979; Shane 1990 b; Brager 1993; Hanson and Defran 1993), as well as other cetacean species (e. g. Norris and Dohl 1980 b; Würsig and Würsig 1980; Klinowska 1986). Data on the diurnal variability in abundance, density or distribution of the inshore prey resources in Algoa Bay are, however, scarce. The only reported fluctuation in the biomass of fish in the surf zone of Algoa Bay is thought to be related to the tidal cycle and increases during low tide; while the species diversity apparently increases just after twilight (Lasiak 1982, 1984). A better understanding of the diurnal cycles of the inshore fish and squid species in Algoa Bay could contribute substantially to our understanding of humpback dolphin diurnal activity/behaviour patterns.

Feeding was the only behaviour of humpback dolphins apparently affected by the tides in Algoa Bay. However, the increase in feeding during high tide in Algoa Bay was less evident than that reported by Saayman and Tayler (1979) in Plettenberg Bay. Saayman and Tayler (1979) speculated that an apparent increase in shoaling behaviour of some reef associated prey species during high tide could increase their "relative accessibility" for dolphins and consequently shape the entire daylight activity pattern of humpback dolphins. This appears less so in Algoa Bay where the biomass of fish in the surf zone is reported to increase at low tide (Lasiak 1982, 1984).

Several other studies conducted in a number of coastal habitats showed various degrees of influence of the tidal cycle on dolphin movement and activity (e. g. Würsig and Würsig 1979; Shane 1990 b: Hanson and Defran 1993; Felix 1994). It seems apparent that the influence of tides, although relatively strong in enclosed bays, passes and narrow channels, generally decreases with the openness of habitat. As the Algoa Bay region is a part of an exposed coastline where wave energy is considerably greater than tidal energy, a limited tidal impact on dolphin activity/behaviour could be expected.

Overall, humpback dolphin behaviour appears similar to that described for other coastal dolphin species like the bottlenose dolphin. The present study, however, was not designed to be strictly behavioural; data on dolphin behaviour were collected opportunistically, as part of a larger scale research project. Consequently, a clear understanding of the behaviours of humpback dolphins and the relevance of these to the fulfilment of their biological and social needs requires further investigation.

Acknowledgements

This work would not have been possible without the financial assistance of the Foundation for Research Development (FRD), WWF South Africa and the University of Port Elizabeth, which is gratefully acknowledged. We wish to express our thanks to Meredith Thornton, Jimmy Henderson, and Shane Norris for their help during fieldwork. We thank Randall Wells (Dolphin Biology Research Institute, Mote Marine Laboratory, Sarasota, Florida, USA), Bernd Würsig (Texas A & M University at Galveston, USA), Anton McLachlan and Deo Winter (University of Port Elizabeth, South Africa) and anonymous reviewers for their comments on the earlier draft of the manuscript; and Nina Wozniak (German Department, University of Port Elizabeth) for her help with translation of Zusammenfassung.

Zusammenfassung

Tagesgang im Verhalten von Buckeldelphinen Sousa chinensis in Algoa Bay, Südafrika

Daten zum Tagesverhalten von Buckeldelphinen *Sousa chinensis* wurden über einen Zeitraum von drei Jahren in der Algoa-Bucht, Ostkapprovinz, Südafrika, in Aufnahmen auf See und vom Land aus erstellt. Die Aktivitäten und Verhaltensweisen der Delphine wurden eingeteilt in: „Nahrungsaufnahme", „Fortbewegung", „opportunistische Nahrungsaufnahme", „gesellschaftliches Verhalten und Spiel", „Ausruhen" und „Anderes". Das Verhalten der Buckeldelphine bestimmt die räumliche Geometrie der Delphingruppe, nicht aber die Gruppengröße. Die Intervalle des Einatmens an der Wasseroberfläche sind ähnlich bei „Nahrungsaufnahme", „opportunistischer Nahrungsaufnahme" und bei langsamer „Fortbewegung", weichen jedoch stark von dem Verhaltensmuster bei schneller „Fortbewegung" ab. Das Tagesverhalten des Buckeldelphins wird von der „Nahrungsaufnahme" dominiert und weist eine starke Regelmäßigkeit auf, die wahrscheinlich von den Tageszyklen der Beutetiere gesteuert wird. Allgemein hat die „Nahrungsaufnahme" morgens ihren Höhepunkt und nimmt im Laufe des Tages allmählich ab. Während die „Nahrungsaufnahme" abnimmt, nehmen „Fortbewegung" und „opportunistische Nahrungsaufnahme" zu und zeigen am Nachmittag gleichsam Höchstwerte. Die Frequenz der Aktivitäten „Ausruhen" und „gesellschaftliches Verhalten und Spiel" bleibt ganztägig etwa gleich, ist aber morgens und abends etwas geringer. Dieses Verhaltensmuster variiert nur geringfügig zwischen Sommer und Winter, ebenso wie das gesamte Verhältnis der Tagesverhaltensweisen. Der einzige bemerkenswerte Unterschied für die Jahreszeiten ist die Frequenz des „gesellschaftlichen/Paarungsverhaltens", das im Sommer seinen Höhepunkt hat. Daraus scheint hervorzugehen, daß die Gesamtproportion der Tagesverhalten der Delphine von ihrem Habitat und ihren biologischen Bedürfnissen determiniert wird. Obwohl der Gezeitenzyklus das Verhalten der Buckeldelphine in einigem Maße beeinflußt, sind Tagesaktivitäten und -verhalten vornehmlich von der Tageszeit bestimmt. Bei zukünftigen Forschungsaufgaben sollten nächtliches Verhalten wie auch das Verhältnis zwischen verschiedenen Verhaltensformen und potentiellen Störfaktoren berücksichtigt werden.

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